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Dietary patterns of *Pseudoeurycea leprosa* (Caudata, Plethodontidae) from Río Frío, Mexico

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The diet of the Mexican plethodontid salamander *Pseudoeurycea leprosa* was found to vary depending on season and size class. Although arthropods comprised the overall majority of the diet, gastropods and oligochaetes occupied a relatively large proportion of the selected prey. Because of their size and moist surface, oligochaetes are not caught successfully by tongue projection, and the jaws may be used to capture such prey. An ontogenetic change in head shape was observed in *P. leprosa*. Juveniles have a proportionally wider head than adults, allowing them to utilize a wider range of prey. A large overlap in diet among size classes was found but this could be attributed to a relatively greater preference for small prey in large individuals and not to the ability of small individuals to ingest large prey. Shorter heads in juveniles could be a way to reduce space within the terrestrial egg and not a way to utilize a broader trophic niche in juvenile salamanders. Despite a pronounced seasonal variation in precipitation in the highlands of central Mexico, diet overlap among seasons was high. This overlap might be attributed to small sample sizes during the dry season or to microhabitat utilization.

Introduction

Salamanders of the family Plethodontidae are unique among urodeles in that a large proportion of the family members occur in the tropical zones of Latin America. The family is represented in the neotropics exclusively by the supergenus *Bolitoglossa* within the tribe Bolitoglossini, which also includes the temperate zone genera *Batrachoseps* and *Hydromantes*.

Despite the interest in the systematics of the group, virtually nothing is known about dietary patterns of neotropical plethodontid salamanders. Because of tongue structure and jaw development, Lombard & Wake (1977) assumed arthropods are the principal prey of this group. A brief note by Vilchis (1990) listed the diet of *Pseudoeurycea leprosa* in the Ajusco mountain range of central Mexico, confirming that arthropods were the principal prey.

In this paper, I present data on seasonal and body size correlates of the diet of the Mexican plethodontid *Pseudoeurycea leprosa*. Several factors might theoretically affect the diet of this species.

(1) Salamanders of the supergenus *Bolitoglossa* possess a remarkable feeding apparatus consisting of a specialized tongue projection system. Morphological and neurological adap-

tations have given these salamanders the ability to capture prey accurately from large distances and at remarkable speed with a free projectile tongue (LOMBARD & WAKE, 1977, ROTH & WAKE, 1985*a-b*). Capture, from onset of protractor muscle activity to tongue contact with the prey target, was recorded at 10 ms for *Bolitoglossa occidentalis*, which gives these salamanders one of the fastest feeding mechanisms among vertebrates (THEXTON et al., 1977). The jaws are relatively poorly developed and tongue projection may be the exclusive feeding mechanism (LOMBARD & WAKE, 1977). These factors combined make the salamanders specialists in capturing small, fast arthropods but make them less suited for capturing large and moist prey like slugs and earthworms. Therefore, arthropods are expected to be the exclusive diet of *P. leprosa*.

(2) The feeding apparatus is not the only morphological factor affecting diet. FRASER (1976) found a significant correlation between head width and size of largest ingested prey in two temperate zone species, *Plethodon cinereus* and *Plethodon hoffmani*. MAGLIA (1996) found that head width limits prey selection in *P. cinereus* and that juveniles compensate somewhat by having relatively wider heads than adults, thereby providing them with a broader trophic niche than would have been the case if no ontogenetic change in head shape occurred. If a similar uneven growth in head width/length were found in *P. leprosa*, a high diet similarity between adults and juveniles would be expected.

(3) Salamanders are generally regarded as being insectivorous opportunistic feeders. If seasonal variation affects prey availability, then this would affect the composition of salamander diet. Seasonal variation may also impair salamander foraging, because plethodontid salamanders are restricted to areas of high humidity. This probably limits the foraging range of the salamanders when outside conditions are dry, perhaps limiting them to their covers or to fossorial foraging (MATHIS et al., 1995). Because there is pronounced seasonal variation in precipitation in the highlands of central Mexico, the overlap in diet between wet and dry season is expected to be low.

MATERIAL AND METHODS

I collected salamanders in the pine-fir forests surrounding the small town of Río Frío on the state border of Mexico and Puebla, Mexico. The area was visited in July-August 1996, October-November 1997 and March-April 1998.

I located specimens by searching potential cover objects during the day. Salamanders were anaesthetized within 1-2 hours of collecting by submersion in a chlorobutanol solution and preserved in 70 % ethanol. Within a few months of preservation, the following measurements were taken: standard length (SL: tip of snout to posterior margin of vent), head length (HL: tip of snout to gular fold) and head width (HW: width of head just behind the eyes). Measurements were made using dial calipers to nearest 0.1 mm. Salamanders were divided into groups according to size and season.

After preservation, the stomachs were removed by dissection and the contents were separated and identified to order. Length and greatest diameter were measured using a binocular microscope with an ocular micrometer to nearest 0.01 mm. Volumes of individual prey items were estimated using the formula for a prolate spheroid (Vitt & Carvalho, 1992):

$$V = 4/3\ \pi\ (\text{length}/2) \times (\text{width}/2)^2.$$

Relative volume (percentage of total volume), relative abundance (percentage of total number) and frequency of occurrence (percentage of stomachs containing a certain category of prey) were calculated for each prey category. The sum of the above was used to calculate an index of Importance Value (IV) (Acosta, 1982):

$$IV = V'_{ij} + N'_{ij} + F'_{ij},$$

where

$V'_{ij} = V_{ij}/\Sigma V_{ij}$,
$N'_{ij} = N_{ij}/\Sigma N_{ij}$,
$F'_{ij} = F_{ij}/N_j$,
IV = Importance Value (I_a of Acosta, 1982),
V_{ij} = Volume of prey items in the i'th category in predator j,
ΣV_{ij} = Total volume of prey items in predator j,
N_{ij} = Number of prey items in the i'th category in predator j,
ΣN_{ij} = Total number of prey items in predator j,
F_{ij} = Number predator j where prey items in the i'th category is present,
N_j = Total number of predator j.

The index provides values between 0 and 300 and gives an estimate of the overall importance of a prey category in a given predator category. The index has the advantage of incorporating more than one measure of importance, but has the disadvantage of giving similar values for different combinations of the three relative values, i.e., each index value is not unique. Another disadvantage with the index is that by incorporating the frequency of occurrence by summation, this measure is often weighted disproportionately more than the other two measures of importance. This is especially the case when sample sizes are small. Since the values for frequency of occurrence do not sum to 100, the index values cannot be used to calculate niche breadth or overlap. Despite such disadvantages, the index was used due to a lack of other indexes incorporating all three measures of importance.

Niche breadth was calculated using the Shannon Index:

$$H_N = -\Sigma P_i \ln P_i,$$

where P_i is the proportion by number of prey items in the i'th category. Niche breadth is greatest if each prey item belongs to a different prey category and lowest if all prey items belong to only one prey category. Another niche breadth (H_V) was calculated using the same index, where P_i is the proportion by volume of prey items in the i'th category. Here niche breadth is greatest if each prey item has the same volume and belongs to a different prey category and lowest if all prey items belong to only one prey category. The Shannon Index was chosen over the more commonly used Simpson's index (Pianka, 1973) because it is less sensitive to the frequency of dominant prey items and to the casual ingestion of prey items (May, 1975).

Pianka's improved index (Pianka, 1975) was chosen for measuring niche overlap:

$$\alpha = \Sigma P_{ij} P_{ik} / \sqrt{(\Sigma P_{ij}^2\ \Sigma P_{ik}^2)}.$$

where P_{ij} and P_{ik} are the proportions of prey items in the i'th category in predator j and predator k, respectively. The index is used solely to show similarity in diet among size- and seasonal groups. Trophic niche breadth was measured using both prey number and volume. The volumetric percentages used were the volumes occupied by each prey taxa, i.e., volumes were not grouped based on individual prey sizes but as total volumes of each prey taxa.

Most of the collected material has been deposited in the collections of the Zoological Museum of Copenhagen, Denmark.

RESULTS

From 1996 to 1998, a total of 93 *P. leprosa* was collected. Six (6.5 %) specimens were collected in spring, 56 (60.2 %) in summer and 31 (33.3 %) in autumn. Seasonal differences in the number of collected salamanders reflect the ease with which salamanders could be located in the field.

PREY COMPOSITION

A total of 301 prey items divided into 17 prey taxa was found in the diet of *P. leprosa*. Of these, 94.4 % (by number) were arthropods and 5.6 % belonged to the orders Oligochaeta and Gastropoda. The numerically most important arthropod prey consisted of springtails (23.3 %), spiders (12.6 %), mites (9.6 %) and beetles (8.6 %). The proportion of arthropod prey by volume was distinctly lower (84.3 %). The volumetrically most important arthropod prey consisted of earwigs (20.0 %), millipedes (16.4 %) and spiders (12.0 %). The overall most important arthropod prey were springtails (IV = 56.9), spiders (IV = 50.4) and beetles (IV = 40.5). Most of the oligochaetes were earthworms of a substantial size. The few gastropods ingested were all snails.

VARIATION IN DIET AMONG SIZE GROUPS

Head width (HW) and head length (HL) of the salamanders showed a positive relationship with standard length (SL) and were highly correlated. Pearson's correlation, r = 0.974 (HL) and r = 0.973 (HW). The slopes of both lines deviated significantly from zero. HW, t-test, t = 40.019, $P < 0.001$; HL, t-test, t = 41.042, $P < 0.001$. The difference between the slopes of the regression lines of HL and HW over standard length was highly significant (t-test, t = 16.141, $P < 0.001$) (fig. 1). The slope of the regression line between head length and standard length suggests that an ontogenetic change in head shape occurs in *P. leprosa* with juveniles having proportionally broader heads than adults.

The correlation (after $\log_{10}$ transformation of both parameters) of HW and volume of largest ingested prey item was highly significant (Spearman Rank Correlation Coefficient, r_s = 0.502, $P < 0.01$), the slope of the line deviated significantly from zero (t-test, t = 9.977, $P < 0.001$) (fig. 2). A similar exponential relationship was found between SL and volume of largest ingested prey item. The slope of the regression line (after $\log_{10}$ transformation) deviated

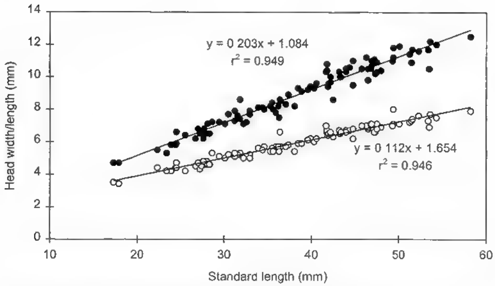

Fig. 1. – Relationship of head length (HL = ●) and head width (HW = ○) to standard length of *Pseudoeurycea leprosa* (n = 93) from Rio Frío, Mexico.

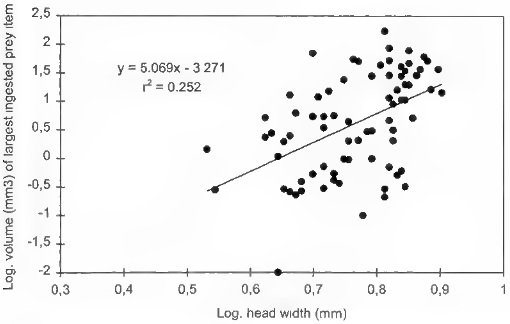

Fig. 2. – Relationship of head width to volume of largest prey item ingested by *Pseudoeurycea leprosa* after $\log_{10}$ transformation (n = 76).

Table 1 Variation in diet among size groups 1, volumetric percentage, 2, numeric percentage, 3, frequency of occurrence; 4, Importance Value (IV). L, larvae. *n*, sample size.

	< 30 mm $n = 20$				30 - 45 mm $n = 48$				≥ 45 mm $n = 25$			
Prey taxa	1	2	3	4	1	2	3	4	1	2	3	4
Blattodea					0.5	0.7	2.1	3.3				
Dermaptera					21.8	7.1	18.8	47.7	19.8	6.0	24.0	49.8
Hemiptera	0.3	1.7	5.0	7.0	0.2	0.7	2.1	3.0	0.3	2.0	8.0	10.3
Coleoptera	15.6	8.3	20.0	43.9	5.3	6.4	14.6	26.3	17.2	12.0	32.0	61.2
Coleoptera (L)	4.3	3.3	5.0	12.6	1.8	5.0	12.5	19.3	2.7	8.0	24.0	34.7
Diptera	0.4	1.7	5.0	7.1	0.2	3.5	6.3	10.0	0.1	2.0	8.0	10.1
Diptera (L)					0.6	4.3	8.3	13.2	0.3	5.0	8.0	13.3
Lepidoptera (L)	1.9	1.7	5.0	8.6	25.4	12.1	8.3	45.8	6.1	2.0	4.0	12.1
Hymenoptera	1.0	5.0	10.0	16.0	1.2	7.8	16.7	25.7	0.6	6.0	16.0	22.6
Collembola	9.7	36.7	40.0	86.4	0.5	15.6	27.1	43.2	1.4	26.0	36.0	63.4
Diplopoda					22.3	5.7	10.4	38.4	11.9	7.0	24.0	42.9
Chilopoda	8.8	1.7	5.0	15.5	4.2	2.8	8.3	15.3	1.9	3.0	8.0	12.9
Pseudoscorpiones					0.3	0.7	2.1	3.1				
Araneae	24.9	15.0	30.0	69.9	5.3	12.1	20.8	38.2	17.5	12.0	32.0	61.5
Acarina	4.1	20.0	40.0	64.1	0.3	9.9	16.7	26.9	0.1	3.0	12.0	15.1
Oligochaeta	21.2	1.7	5.0	27.8	9.8	4.3	12.5	26.6	20.1	6.0	16.0	42.1
Gastropoda	7.7	3.3	10.0	21.0	0.4	1.4	4.2	6.0				
Prey diversity	H_v 2.030		H_n 1.902		H_v 1.978		H_n 2.558		H_v 1.987		H_n 2.349	

significantly from zero (*t*-test, $t = 4.047$, $P = 0.001$). Although significant, the correlation was slightly lower (Spearman Rank Correlation Coefficient, $r_s = 0.472$, $P < 0.01$) than for the relationship between HW and prey volume. Prey selection by size seems best to be described by salamander head width.

Niche breadth was similar for all size groups (tab. 1). The lowest was found in the smallest salamanders and the highest in the intermediate size group. When judged by prey number, diet overlaps were high and similar among the three size groups. The highest overlap was between the largest and the intermediate size groups ($\alpha = 0.887$) and the smallest between the intermediate and the smallest size groups ($\alpha = 0.802$).

Diet overlaps were distinctly lower when judged by prey volume and the range in overlap among size groups was much higher. The highest overlap was between the largest and the smallest size groups ($\alpha = 0.747$) and the smallest between the intermediate and the smallest size groups ($\alpha = 0.312$). The high trophic overlap between the smallest and the largest salamanders can best be attributed to small sample sizes but does suggest high diet similarity among the different sizes of *P. leprosa*.

The importance of different prey taxa varied among salamander size groups as a function of prey size (tab. 1). Mites were among the three most important prey taxa in the smallest size group, but as salamander size increased mites became less important. Large prey (e.g., earwigs and millipedes) did not occur in the diet of the smallest salamanders, but became increasingly important in the larger salamander size groups.

Other prey taxa did not show any apparent variation in diet of smaller and larger salamanders. Although most important in the diet of the smallest salamanders, springtails continued to be of a high importance in the diet of the largest salamanders. A similar situation was found for spiders, beetles and hymenopterans.

Seasonal variation

One stomach (16.7 %) was empty in spring, 11 (19.6 %) in summer and five (16.1 %) in autumn. This suggests no shortage of prey during the drier months.

Niche breadth was similar for summer and autumn but markedly lower in spring, although this may be due to the low number of stomachs sampled (tab. 2). Diet overlap in prey number was high among seasons. The highest overlap ($\alpha = 0.804$) occurred between spring and summer, and the lowest overlap between spring and autumn ($\alpha = 0.669$). Niche breadth in general was much lower when diet overlap was judged by prey volume. The highest overlap occurred between summer and autumn ($\alpha = 0.397$) and the lowest between spring and summer ($\alpha = 0.121$). Due to the volumetric dominance of a single very large prey item in the spring sample, overlaps judged by volume involving this season are most likely to be underestimated.

Mean number of ingested prey items varied slightly among seasons: 1.33 prey items/stomach (spring), 3.68 (summer) and 2.77 (autumn). Even if empty stomachs are omitted, the variation in number of ingested prey items among seasons is not significant (ANOVA, $F_{2, 73} = 3.011$, $P = 0.055$).

The three most important prey in spring were centipedes, spiders and springtails (tab. 2). Due to the low number of salamanders found at this season, these data must be viewed with caution. The high importance value (IV) reported for centipedes can be referred to a single ingested item of a very large size. Its high importance is, therefore, questionable. More reliable are the importance values for spiders and springtails which were found in one third of all stomachs. Spiders and springtails may be regarded as the most important prey taxa for *P. leprosa* in spring.

Only in the summer sample were all 17 prey taxa found. Springtails, earwigs, beetles and spiders were the most important prey taxa. Despite occupying a low proportion of overall prey volume, springtails were found in almost one third of all stomachs and occurred in high numbers, making them the most important prey item in the summer sample. Earwigs were found in low numbers in the stomachs but at a relatively high frequency. Both beetles and spiders were intermediate in respect to volume, number and frequency.

The most important prey in the autumn sample were caterpillars, spiders, springtails and millipedes. The importance of caterpillars as prey is due to a large volume and high numbers, despite a relatively low frequency in the stomachs. This prey seems to be both patchily

Table 2. Seasonal variation in diet. 1, volumetric percentage; 2, numeric percentage; 3, frequency of occurrence; 4, Importance Value (IV). L, larvae. *n*, sample size

	Spring $n = 6$				Summer $n = 56$				Autumn $n = 31$			
Prey taxa	1	2	3	4	1	2	3	4	1	2	3	4
Blattodea					0.4	0.4	1.8	2.6				
Dermaptera					27.3	7.1	23.2	57.6	4.0	2.3	6.5	12.8
Hemiptera					0.6	2.1	7.1	9.8				
Coleoptera	5.9	12.5	16.7	35.1	19.4	10.5	25.0	54.9	2.2	5.8	12.9	20.9
Coleoptera (L)					4.9	9.5	23.2	37.6				
Diptera	1.6	12.5	16.7	30.8	0.1	0.8	3.6	4.5	0.2	3.5	9.7	13.4
Diptera (L)					0.1	3.6	3.6	7.3	0.8	7.0	12.9	20.7
Lepidoptera (L)					0.8	0.6	1.8	3.2	35.2	22.1	12.9	70.2
Hymenoptera					1.1	6.3	17.9	25.3	0.4	5.8	12.9	19.1
Collembola	2.1	25.0	33.3	60.4	3.5	24.3	32.1	59.9	0.8	17.4	29.0	47.2
Diplopoda					7.6	3.9	10.7	22.2	23.8	7.0	16.1	46.9
Chilopoda	77.0	12.5	16.7	106.2	0.8	2.4	8.9	12.1	4.7	2.3	6.5	13.5
Pseudoscorpiones					0.3	0.4	1.8	2.5				
Araneae	12.8	25.0	33.3	71.1	15.5	11.4	21.4	48.3	14.3	15.1	32.3	61.7
Acarina	0.7	12.5	16.7	29.9	1.6	11.1	26.8	39.5	0.3	5.8	9.7	15.8
Oligochaeta					12.8	4.3	12.5	29.6	13.1	4.7	9.7	27.5
Gastropoda					3.5	1.4	5.4	10.3	0.1	1.2	3.2	4.5
Prey diversity	H_v		H_n		H_v		H_n		H_v		H_n	
	0.813		1.733		2.080		2.383		1.746		2.279	

distributed (a single stomach contained 13 prey items all referable to Lepidoptera) and seasonal in its abundance (IV = 3.2 in summer sample).

DISCUSSION

In the plethodontine genera *Aneides* and *Plethodon*, arthropods constitute by number more than 90 % of the diet and somewhat less by volume (POWDERS & TIETJEN, 1974; FRASER, 1976; LYNCH, 1985; MAGLIA, 1996). Within the bolitoglossines, arthropods comprised more than 90 % of the diet of *Batrachoseps attenuatus* (MAIORANA, 1978) and *Speleomantes ambrosii* [*Hydromantes strinatii*] (SALVIDIO, 1992). The proportion of arthropods in the diet of *Pseudoeurycea leprosa* is similar to these two species when judged by number but distinctly lower when judged by volume. Snails can easily be caught with tongue projection, as the tongue pad can glue to the dry shell. Snails occur regularly in the diet of all the above mentioned species. The moist surface of earthworms makes the tongue pad less adhesive and makes capture with tongue projection difficult The relatively large proportion and large individual size of oligochaetes in the diet of *P. leprosa* suggest that the jaws are used in prey capture, at least to a limited extent in this species. This is in contrast to the interpretation by LOMBARD & WAKE (1977) who assumed that the weak jaws made tongue projection the exclusive feeding mechanism. Earthworms were found in the diet of *Speleomantes ambrosii* [*Hydromantes strinatii*] (SALVIDIO, 1992), whereas only snails comprised the non-arthropod prey in *Batrachoseps attenuatus* (MAIORANA, 1978). No data are currently available on the behavior of capture of large moist prey in Bolitoglossini, although they are highly desirable.

In a study of feeding ecology in the temperate zone species *Plethodon cinereus*, MAGLIA (1996) found a high degree of similarity in the diet of juveniles and adults. As reported for other species of *Plethodon* (e.g., FRASER, 1976), head width was significantly correlated with prey size and an ontogenetic variation in head shape occurred, with juveniles having proportionally broader heads than adults. Thus, MAGLIA (1996) concluded that in terrestrial salamanders an ontogenetic change in head morphology results in a lack of change in diet, whereas a lack of change in head morphology results in a diet change. *Pseudoeurycea leprosa* appears to fit this model Head width was significantly correlated with prey size and the diet of the three size groups overlapped extensively The similarity in diet between small and large specimens of *P leprosa* does not seem to be attributed to the ability of small salamanders to ingest large prey It is more likely a higher preference by the larger salamanders for smaller prey, as evidenced by the high proportion of prey like springtails and hymenopterans in the diet of larger *P. leprosa*.

Ontogenetic change in head shape contributes to the lack of diet change in *P cinereus* The results obtained for *P. leprosa* might differ due to a lower sample size (93 *P leprosa* versus 348 *P. cinereus*), but I do not consider this a viable explanation In some species of plethodontid salamanders with direct development, juveniles hatch with a tail proportionally shorter than adults, and an ontogenetic change in tail length occurs (e.g., *Bolitoglossa mexicana* BILLE & BRINGSØE, 1998) This situation is similar to the reported changes in head shape and may be a way to reduce space within the terrestrial egg I hypothesize that a shorter head could be another way to reduce space within the egg and not a way to utilize a broader trophic niche for juvenile salamanders. Although in some species like *P cinereus* this might be the result, the basis is different and generalizations should be avoided

Because terrestrial plethodontids are opportunistic feeders, seasonal variation in diet should be expected when prey abundance and diversity varies over the year. Seasonal differences in diet have been reported for *Plethodon glutinosus* and *Plethodon jordani* (POWDERS & TIETJEN, 1974) Salamander foraging might also be impaired when outside conditions are dry thereby limiting the foraging range of the salamanders. When leaf litter is dry, *Plethodon cinereus* is confined to foraging in their covers which limits prey amount and diversity (JAEGER, 1980). The highlands of central Mexico experience a pronounced seasonal variation in precipitation, and even if prey abundance and diversity are not affected by the seasons, niche breadth of the salamanders would be expected to be much lower in the dry season due to limited foraging opportunities. The high seasonal overlaps found in *P leprosa* are therefore surprising Although a slight seasonal variation in prey taxa was encountered, the differences were insignificant The driest situations occurred in spring which unfortunately coincided with the smallest sample size A different situation might have appeared, had the sample been larger Another explanation could be the condition of the cover types selected by the species. *Pseudoeurycea leprosa* is mainly log-dwelling (sensu WAKE & LYNCH, 1976) and the most popular cover type is under the loose bark on fallen logs. This extensive cover, often of several meters length, provides the salamanders with a relatively large foraging range compared to other cover types. During the dry season this cover is utilized only to a limited extent and explains therefore only a small part of the high similarity in diet.

RESUMEN

Se describe la variacion en la dieta de la salamandra plethodóntida mexicana *Pseudoeurycea leprosa* a lo largo de estaciones del año y entre clases de tamaños. Aunque los artrópodos constituyen la mayor parte de la dieta, los gastropodos y los oligoquetos ocupan una proporción relativamente grande entre las presas seleccionadas. Debido a su tamaño y a su superficie húmeda, se da por sentado que los oligoquetos no pueden ser capturados mediante la proyección de la lengua y, contrariamente a las expectativas anteriores, se supone que se utilizan básicamente las mandíbulas en la captura de tales tipos de presa. En otros plethodóntidas terrestres se ha observado un cambio ontogenético en la forma de la cabeza, y algo similar podría ocurrir con la *P leprosa*; por ejemplo los juveniles tienen la cabeza proporcionalmente más ancha que los adultos. Ésto se ha atribuído a la la posibilidad de permitir a los juveniles utilizar una más amplia gama de presas que si no hubiese producido dicho cambio en la forma de la cabeza. Se encontró una gran superposición en las respectivas dietas de las clases de tamaños pero ésto podría atribuirse a una preferencia relativamente grande de los individuos grandes por presas pequeñas y no la habilidad de ingerir grandes presas por parte de los individuos pequeños. El autor lanza la hipótesis de que la cabeza más corta en los juveniles podría ser una adaptacion para ahorrar espacio dentro del huevo terrestre, y no una adaptación a un nicho trófico más amplio por parte de las salamandras jóvenes. A pesar de la gran variacion de las precipitaciones de las tierras altas del centro de México en las distintas estaciones del año, que restringe severamente el espectro alimenticio de las salamandras en la temporada seca, la superposición dietaria en las estaciones del año resultó ser elevada Ésto podría ser atribuído al pequeño tamaño de las muestras durante la temporada seca o podría ser debido al uso del micrihábitat por parte de esta especie.

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